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Environmental factors influencing the distribution of endangered endemic species *Hedysarum criniferum* Boiss in arid and semi-arid rangelands, Iran

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Abstract: Understanding the factors influencing the distribution of plant species is crucial for enhancing the management of endangered ecosystems. This study investigated the response of *Hedysarum criniferum* Boiss, an endemic and endangered species to 25 environmental variables within its habitats with an area of 2.95×10^5 km² in arid and semi-arid rangelands of Iran. The purpose of this research is to identify the key environmental factors affecting the distribution and habitat preferences of *H. criniferum* for further conservation and restoration of the species. To predict the occurrence of *H. criniferum* and explore its relationship with environmental factors, we employed the best subset regression analysis, the hierarchical classification, and the extended Huisman-Olf-Fresco (eHOF) model. The results showed that four environmental variables, i.e., gravel content, pH, annual minimum temperature, and mean annual temperature showed significant correlations with the canopy cover of *H. criniferum* ($P<0.05$). The probability of *H. criniferum* occurrence increased with higher precipitation and elevation, while it decreased with higher mean annual temperature, annual minimum temperature, and gravel content. The species' response curves and their optimal values, as assessed by the eHOF model, indicated that the response to mean annual temperature, ranging from 12°C to 16°C, was optimal at 13°C. The response to mean annual precipitation, within a range of 150–650 mm, was optimal at 650 mm. Elevation responses, spanning from 1546 to 2450 m, showed an optimum at 2450 m. Regarding soil characteristics, the response to gravel content, ranging from 13.0%–48.0%, demonstrated an optimal value at 20.0%. The pH levels, varying from 7.5 to 8.2, prompted a sine-shaped response with an optimal pH of 8.0. These findings provide valuable insights for predicting species occurrence and identifying suitable locations for restoration programs. Our study underscores the importance of considering multiple environmental variables in habitat suitability assessments. By incorporating these broader considerations, we can further refine predictive models and enhance conservation efforts aimed at restoring habitats conducive to the luxuriance of endangered species like *H. criniferum*.

Keywords: habitat suitability; species response curves; best subset regression; extended Huisman-Olf-Fresco (eHOF) model; hierarchical classification

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1 Introduction

Recognizing the influence of environmental changes on plant species distribution is crucial, especially in semi-arid areas characterized by diverse climatic, topographic, and soil properties that contribute to distinct plant habitats (Schroeder et al., 2010; Michaelis and Diekmann, 2017). These varied environmental factors act as sensitive indicators, reflecting the specific needs of each species. Understanding how these environmental factors interact and affect plant species distribution is essential for effective conservation and management strategies in such dynamic ecosystems.

Various models have been employed to study plant response curves. Traditional models such as bioclim, biomod, generalized additive model (GAM), and logistic regression (LR) have provided valuable insights, yet they have inherent limitations (Santika and Hutchinson, 2009). Previous studies have highlighted problems with the assumption of a symmetric shape in LR and have noted difficulties in the interpretation and application of GAM (Oksanen and Minchin, 2002; Heikkinen and Mäkipää, 2010). Additionally, generalized linear model (GLM) may produce biologically unrealistic response curves. Incorrect assumptions about functional relationships can lead to biased estimations and erroneous conclusions (Heegaard, 2002; Austin, 2007). Some studies have suggested that plant species exhibit varied responses to environmental factors, such as unimodal and Gaussian or diagonal and uniform response curves (Lawesson and Oksanen, 2002; van der Veen et al., 2021).

Recent reseraches have led to the development of the extended Huisman-Olff-Fresco (eHOF) model, which addresses the drawbacks of previous models and provides a reliable fit for analyzing vegetation cover (Huisman et al., 1993; Jansen and Oksanen, 2013; Bartholomée et al., 2023). However, despite these studies, gaps persist in understanding how plant species respond to ecological gradients, particularly for endangered species with a clumped distribution, such as *Hedysarum criniferum* Boiss, an endemic and valuable species in Iranian semi-arid rangelands. *H. criniferum* is a valuable and perennial forb from the Fabaceae family that grows in the cold steppe zone of the Irano-Turanian floristic region (Choi et al., 1999; Shahbazi et al., 2017). While previous studies, such as that by Hayati et al. (2022), employed principal component analysis (PCA) to identify the most critical factors influencing *H. criniferum* distribution, these methods often fail to capture the nonlinear and complex interactions between environmental variables. Additionally, the GLM method used by Hayati et al. (2022) assumes linear relationships, which may oversimplify the species' responses to environmental gradients and overlook potential synergistic effects (Anderson et al., 2022).

This paper adopts a different approach, utilizing the best subset regression analysis and hierarchical partitioning (HP) to identify the key environmental factors influencing the distribution of *H. criniferum*. We hypothesize that employing a combination of linear and nonlinear methods will provide a more comprehensive understanding of the factors shaping the habitat of *H. criniferum*. The specific objectives of this study are to: (1) identify the primary environmental factors influencing *H. criniferum* through the best subset regression; (2) assess the significance of each identified factor using HP; and (3) evaluate the response curve of the species to climatic factors, topography, and soil characteristics using the eHOF model, and compare the result with that reported by the GLM method (Hayati et al., 2022).

2 Materials and methods

2.1 Study area

The study area is located in western and southwestern Iran. The natural 8 habitats (Shahbazi et al., 2017) of *H. criniferum* with an area of 2.95×10^5 km^2 were selected (29°53′25″–35°34′35″N, 46°21′37″–51°57′36″E; Fig. 1). The climate of the study area is predominantly classified as cold semi-arid, characterized by distinct seasonal variations. Key climate parameters include mean annual temperature ranging from 12°C to 16°C and mean annual precipitation varying between

150 and 650 mm. The altitude of the study area spans from 1546 to 2450 m a.s.l., with slopes ranging from 27.0% to 70.0%. The soils in the area are alkaline, with pH levels between 7.5 and 8.2. Soil organic matter content ranges from 0.2% to 1.2%, and electrical conductivity (EC) varies from 1.6 to 5.3 dS/m. Table 1 provides vital geographical and environmental characteristics of these habitats.

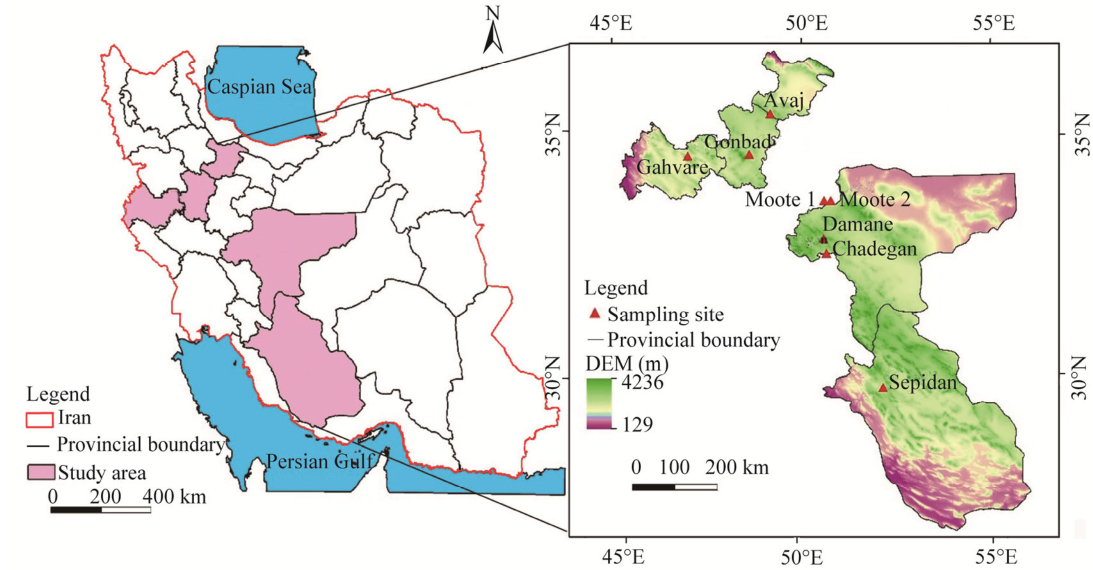

Fig. 1 Geographical location of the natural habitat sites of *Hedysarum criniferum* Boiss in Iran. DEM, digital elevation model.

Table 1 Main features of selected natural habitats sites of *H. criniferum* in Iran

Site number	Site name	Province	Latitude	Longitude	Elevation (m)	Slope (%)	Mean annual precipitation (mm)
1	Sepidan	Fars	29°53′25′′N	51°57′36′′E	2050	45.0	560
2	Damane	Isfahan	33°00′14′′N	50°37′01′′E	2450	60.0	550
3	Moote 1	Isfahan	33°47′00′′N	50°47′30′′E	1943	70.0	150
4	Moote 2	Isfahan	33°46′58′′N	50°46′24′′E	2090	65.0	150
5	Chadegan	Isfahan	33°42′25′′N	50°28′18′′E	2114	70.0	343
6	Avaj	Ghazvin	34°32′23′′N	49°12′50′′E	2118	45.0	412
7	Gahvare	Kermanshah	34°20′59′′N	46°21′37′′E	1546	33.0	430
8	Gonbad	Hamedan	35°34′35′′N	48°41′46′′E	2266	27.0	329

2.2 Field sampling

To comprehensively assess the environmental factors influencing *H. criniferum* distribution, we divided the factors into different scales: large-scale climatic and geographical factors, mid-scale watershed conditions, and small-scale site-specific information obtained through field sampling. For each habitat, we recorded large-scale climatic data from the nearest weather stations, including mean annual precipitation (MAP), mean wind speed (MWS), maximum wind speed (MxWS), annual maximum temperature (AMT_max), annual minimum temperature (AMT_min), and mean annual temperature (MAT). Elevation data were recorded using a global positioning system (GPS) device. At the mid-scale, physiographical parameters such as geographical direction and slope percentage were assessed using a compass and a laser ruler, respectively. At the small-scale, site-specific soil and vegetation characteristics were determined through

comprehensive soil and vegetation analysis. This structured approach allowed us to assess 25 environmental variables for each habitat, as shown in Table 2.

Table 2 Correlation of environmental factors with plant height and canopy cover of *H. criniferum* in the arid and semi-arid rangelands of Iran

Variable	Abbreviation	Plant height		Canopy cover	
		R^2	P	R^2	P
Gravel	Gr	–0.690	0.000**	–0.620	0.001**
Lime	-	0.050	0.840	–0.320	0.120
Soil organic carbon	SOC	–0.220	0.300	–0.380	0.070
Soil pH	pH	–0.410	0.040*	–0.590	0.002**
Electrical conductivity	EC	–0.640	0.001**	–0.510	0.010*
Soil calcium	Ca	–0.800	0.000**	–0.660	0.000**
Soil magnesium	Mg	–0.530	0.008**	–0.520	0.010**
Soil sodium	Na	–0.670	0.000**	–0.540	0.006**
Soil potassium	K	–0.390	0.060	–0.540	0.007**
Soil phosphorus	P	–0.150	0.470	–0.090	0.690
Soil nitrogen	N	–0.370	0.070	–0.180	0.400
Calcium sulfate	$CaSO_4$	–0.090	0.690	–0.160	0.460
Sodium adsorption ratio	SAR	–0.230	0.280	–0.270	0.270
Sand	-	–0.040	0.840	0.110	0.620
Silt	-	–0.030	0.910	–0.040	0.850
Clay	-	0.090	0.690	–0.130	0.550
Elevation	-	0.630	0.010*	0.590	0.010**
Aspect	-	0.310	0.210	–0.400	0.060
Slope	-	0.020	0.940	–0.370	0.080
Mean annual precipitation	MAP	0.670	0.000**	0.500	0.010*
Mean wind speed	MWS	–0.590	0.003**	–0.510	0.010*
Maximum wind speed	MxWS	0.140	0.520	0.390	0.070
Annual maximum temperature	AMT_max	–0.260	0.230	–0.070	0.750
Annual minimum temperature	AMT_min	–0.710	0.000**	–0.570	0.004**
Mean annual temperature	MAT	0.630	0.002**	–0.620	0.006**

Note: The abbreviations are the same in the following tables and figures. - means no abbreviation. *, $P<0.05$ level; **, $P<0.01$ level.

In May 2019, vegetation cover was assessed using the minimum area method (Mueller-Dombois and Ellenberg, 1974). Quadrat sizes ranged from 2 m^2 (2 m×1 m) to 25 m^2 (5 m×5 m), tailored to suit species distribution in each site. Canopy cover of all *H. criniferum* species was documented within each habitat. The method of Cochran (1977) was used to determine the number of plots in each site. We measured canopy cover by visually estimating the percentage of ground area that was covered by vertical projection of plant canopy within each quadrat. Height was measured using a meter stick or measuring tape, from the base of plant to the highest point of canopy. These measurements were recorded for each plant within the sampled quadrats.

Soil characteristics were evaluated in three randomly chosen plots within each habitat. Four soil samples were collected from rhizosphere zone of *H. criniferum*, at a depth of 0–20 cm, considering active root growth zone for this species. These samples were then combined to form a composite sample, which was subsequently sent to the laboratory to analyze their physical and chemical properties. In total, 24 soil samples were gathered from 8 habitats. We selected soil variables based on previous research and compared soil traits in areas where *H. criniferum* is

present and absent (Sheikhzadeh et al., 2019). These variables were expected to influence the species' distribution.

Soil analysis encompassed a range of parameters, which is crucial for understanding the habitat of *H. criniferum*. The pH of the soil was determined using a glass electrode and the pH meter, while electrical conductivity (EC) was measured with a conductivity meter. Both pH and EC were determined in a 1:5 soil-to-water suspension using the method of McLean (1982). We quantified sodium and potassium ion concentrations through flame-photometry according to the method outlined by Jankowski and Freiser (1961). Additionally, soil organic carbon was assessed using the Walkley-Black method, lime content was determined via titration (Nelson and Sommers, 1996), and soil texture was analyzed using the hydrometer method. Absorbable phosphorus content was measured with a spectrophotometer following the method of Olsen (1954). Gypsum percentage was estimated using the acetone method, and total nitrogen content was determined using the Kjeldahl method (Bremner, 1960).

2.3 Data analysis and modeling

We regarded species height and canopy cover as dependent variables, while environmental parameters at various scales served as independent variables. A thorough analysis was conducted to examine the relationship and correlation between environmental variables and measured parameters of *H. criniferum*. Subsequently, the best subset regression was employed to assess the composite effect of all factors, and the optimal regression model was utilized to predict the measured parameters of *H. criniferum*. To evaluate the collinearity among variables, we conducted a Pearson's correlation analysis specifically on the variables included in the best model. The regression models were developed using the SigmaPlot v.14.0 software package where all possible models were initially generated. We selected the optimal model based on high adjusted R^2 and low Mallows's compactness (Cp). The best regression model, derived from the best subset selection, identified the most influential variables affecting *H. criniferum*. These key variables were subsequently incorporated into models to study the species' response to environmental factors using the eHOF model. To validate the robustness and reliability of our model predicting the occurrence of *H. criniferum*, we employed bootstrapping instead of traditional test data due to the limited availability of independent test data and the species' patchy distribution. We performed bootstrap resampling (n=100) using the eHOF package in R software, creating multiple simulated datasets by repeatedly sampling from the original data with replacement. This approach allowed us to rigorously assess model stability, using deviance, log-likelihood (logLik), and Akaike Information Criterion (AIC) corrected for small sample sizes as evaluation metrics (Dixon, 2020; Burak and Kashlak, 2024). Furthermore, HP was employed to discern the independent impact of each influential factor within the best model. This analysis clarifies the independent and combined contributions of each predictor variable to the total variance in the regression model (Cao and Wang, 2023). HP analysis addresses the common issue of multicollinearity in environmental variables and determines the relative importance of each factor, making it a suitable method for multidimensional environmental research (Mac Nally, 1996). The HP analysis was conducted using the SPSS software package to estimate the percentage of independent impact of predictor variables within the best model.

The original HOF model characterizes species response along environmental gradients through five models, i.e., model I signifies no response, model II depicts a monotone incremental or decremental trend, model III illustrates an increase or decrease trend below a maximum attainable response, model IV demonstrates a symmetrical unimodal response, and model V represents an asymmetrical unimodal response. The original HOF fails to explain specific predictions, particularly bimodal models. To address this limitation, we reiterated the HOF models to include bimodal models in the analysis (Jansen and Oksanen, 2013). Two additional models, labeled VI and VII, were introduced, describing symmetrical bimodal response and skewed relations with two optimal values, respectively. AIC was employed to identify the optimal model for fitting the

species response curve. The model with the lowest AIC was selected as the most suitable. All computations were conducted using R software package with the eHOF package (R Development Core Team, 2015).

3 Results

3.1 Determining the best regression model

The study employed the best subset regression to identify the most influential factors impacting the distribution of *H. criniferum*. Factors that exhibited a significant correlation with the species' distribution were considered for inclusion in the regression model. The analysis revealed that the height of *H. criniferum* demonstrated the strongest correlation with calcium (Ca) content (R^2= –0.800) and AMT_min (R^2= –0.710), while the canopy cover was most closely correlated with Ca content (R^2= –0.660) and gravel content (R^2= –0.620) (Table 3).

The regression analysis for both plant height and canopy cover of *H. criniferum* revealed significant relationships with environmental factors (Table 3). For plant height, the initial model,

Table 3 Regression analysis for plant height and canopy cover of *H. criniferum* with environmental variables

Plant height														
R^2	Adj R^2	MSE (cm)	Cp	Gr	**pH**	EC	Ca	Mg	Na	**Elevation**	**MAP**	MWS	**AMT_min**	MAT
0.639	0.623	61.85	5.899				*							
0.762	0.739	42.81	4.886	*									*	
0.784	0.751	40.82	3.462		*					*			*	
0.806	**0.765**	**38.53**	**0.065**		*					*	*		*	
0.816	0.765	38.50	1.189		*				*	*	*		*	
0.822	0.759	39.52	2.787		*	*		*	*	*			*	
0.829	0.755	40.28	4.268		*	*		*	*	*	*		*	
0.832	0.743	42.17	6.040		*	*	*	*	*	*	*		*	
0.833	0.725	45.12	8.025	*	*	*	*	*	*	*	*		*	
0.833	0.704	48.55	10.015	*	*	*	*	*	*	*	*		*	*
0.833	0.680	52.54	12.000	*	*	*	*	*	*	*	*	*	*	*
Canopy cover														
R^2	Adj R^2	MSE (%)	Cp	**Gr**	**pH**	EC	Ca	Mg	Na	Elevation	MAP	MWS	**AMT_min**	**MAT**
0.440	0.415	70.37	23.560				*							
0.770	0.748	30.35	13.230	*						*				
0.787	0.756	29.39	4.541	*						*				*
0.807	**0.766**	**28.11**	**1.026**	*	*								*	*
0.822	0.772	27.37	1.867	*	*						*		*	*
0.831	0.772	27.46	3.138	*	*				*		*		*	*
0.836	0.764	28.41	4.789	*	*	*			*		*		*	*
0.847	0.765	28.29	5.942		*	*	*		*		*	*	*	*
0.853	0.759	29.00	7.424		*	*	*		*		*	*	*	*
0.856	0.746	30.58	9.188	*	*	*	*		*		*	*	*	*
0.858	0.728	32.65	11.025	*	*	*	*		*	*	*	*	*	*
0.859	0.704	35.54	13.000	*	*	*	*	*	*	*	*		*	*

Note: The optimal model, determined based on the highest R^2 and the lowest Mallows's compactness (Cp) values, is shown in bold. MSE, mean squared error. * indicates the significant correlation between plant height or canopy cover and environmental variable at P<0.05 level.

incorporating all environmental variables, explained 83.3% of the variance with an R^2 of 0.830. However, it also exhibited a high mean squared error (MSE) of 52.535 and a Mallows's Cp value of 12.000, indicating issues with overfitting and model complexity. After applying backward regression to simplify the model, the optimal model emerged with an R^2 of 0.810 and a substantially lower Cp value of 0.065. This refined model, which included pH, elevation, MAP, and AMT_min, provided a better balance between model complexity and explanatory power. Similarly, the initial model for canopy cover had an R^2 of 0.440 and a high Cp value of 23.560, reflecting an overly complex structure. The optimal model for canopy cover, identified through backward regression, achieved an R^2 of 0.807 and a Cp value of 1.026. This model included gravel content, pH, MAP, and AMT_min, highlighting their critical roles in determining canopy cover, with gravel content significantly influencing soil texture and water retention. The lower Cp values in the optimal models for both plant height and canopy cover indicated effective models that efficiently explained the variance in the response variables while avoiding unnecessary complexity.

Regarding the best regression model to predict the height of *H. criniferum*, which includes pH, elevation, MAP, and AMT_min, no significant correlation was observed among these variables (P>0.05). Similarly, for predicting canopy cover, the correlation between gravel, pH, MAP, and AMT_min variables showed no significant correlation (P>0.05) (Table 4).

Table 4 Correlation between variables of the best regression model to predict plant height and canopy cover of *H. criniferum*

Factor	Plant height		
	pH	Elevation	MAT
Elevation	–0.303 (P=0.465)		
MAP	–0.158 (P=0.709)	0.133 (P=0.754)	
AMT_min	–0.398 (P=0.328)	–0.218 (P=0.603)	0.638 (P=0.089)
Factor	Canopy cover		
	Gravel	pH	AMT_min
pH	0.560 (P=0.149)		
MAP	–0.667 (P=0.071)	–0.398 (P=0.328)	
AMT_min	–0.374 (P=0.361)	–0.172 (P=0.685)	–0.136 (P=0.747)

3.2 Environmental factors influencing *H. criniferum* distribution

Results of HP analysis revealed that MAP and AMT_min were the primary contributors, accounting for 48.5% and 28.4% of the variance in *H. criniferum* height, respectively. Additionally, pH and elevation accounted for 21.6% and 1.4% of the variance in plant height, respectively (Fig. 2).

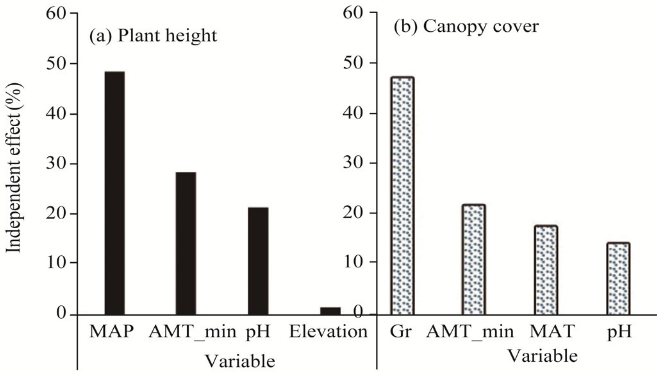

Fig. 2 Results of hierarchical partitioning (HP) analysis for the variances of plant height (a) and canopy cover (b) of *H. criniferum*

For canopy cover, gravel and AMT_min emerged as the most influential factors, explaining 47.0% and 21.8% of the variance, respectively. Furthermore, MAT and soil pH contributed to 17.2% and 14.0% of the variance in canopy cover, respectively (Fig. 2). These findings provide valuable insights into the specific environmental variables that significantly impact plant height and canopy cover of *H. criniferum*.

3.3 Species response curves analyzed by the eHOF models

Through analyzing the species response curves by the eHOF models, we identified 6 factors as pivotal in influencing the distribution of *H. criniferum*. The selected models for categories IV and V with the lowest AIC values were MAP, MAT, AMT_min, and elevation, signifying their appropriateness in fitting the species response curve to these climatic and physiographical variables. For the species response to soil characteristics, models V and IV were deemed the most suitable for gravel and pH, respectively (Table 5). It is noteworthy that all models characterizing the species' response to environmental variables fell under categories IV and V, collectively accounting for 50.0% of the species' response. These outcomes shed light on the nuanced relationship between *H. criniferum* and key environmental factors, providing a comprehensive understanding of its distribution patterns.

Table 5 Akaike information criterion (AIC) values of each model for each environmental variable based on the extended Huisman-Olf-Fresco (eHOF) model

Variable	No response trend (Model I)	Monotone increasing or decreasing trend (Model II)	Increasing or decreasing trend below a maximum attainable response (Model III)	Symmetrical unimodal response (Model IV)	Asymmetrical unimodal response (Model V)	Symmetrical bimodal response (Model VI)	Skewed relations with optimal value (Model VII)
MAT	31.04	21.66	13.61	7.34*	10.36	10.36	13.78
AMT_min	31.04	19.43	17.47	16.81*	18.22	19.83	23.23
MAP	31.04	32.97	28.82	26.52	26.05*	29.54	32.27
Elevation	31.04	31.93	28.06	18.66	18.57*	21.58	24.98
Gravel	31.04	33.47	28.49	23.07	22.67*	26.10	29.49
pH	28.09	26.44	24.40	20.31*	21.69	23.56	27.32

Note: * is the lowest AIC that is selected as the most suitable model.

The response of *H. criniferum* to MAT, ranging from 12°C to 16°C, exhibited a decremental trend (Fig. 3a). On the other hand, its response to MAP, ranging from 150 to 650 mm, showed an incremental-decremental pattern. In contrast, AMT_min, varying between –12°C and –25°C, exhibited a decremental trend (Fig. 3b and c). Similarly, the response to elevation, spanning from 1546 to 2450 m in the habitats, initially showed an increasing trend followed by a decreasing trend (Fig. 3d). Regarding soil characteristics, the response to gravel content, ranging from 13.0% to 48.0%, demonstrated an initial increase and subsequent decrease, while pH, varying from 7.5 to 8.2, prompted a sine-shaped response in *H. criniferum* (Fig. 3e and f).

The optimal points for the response of *H. criniferum* to climatic variables were 13°C for MAT and 650 mm for MAP (Fig. 3a and b). Additionally, the species exhibited optimal occurrence at an elevation of 2450 m (Fig. 3d). Furthermore, in terms of the highest likelihood of presence, *H. criniferum* responded favorably to soil characteristics of 20.0% gravel content and a pH level of 8.0 (Fig. 3e and f). These findings offer detailed insights into the species' specific environmental preferences, which are crucial for predicting its distribution patterns and informing conservation efforts.

4 Discussion

4.1 Environmental determinants of *H. criniferum* distribution

In this study, we investigated the environmental factors affecting the distribution of the

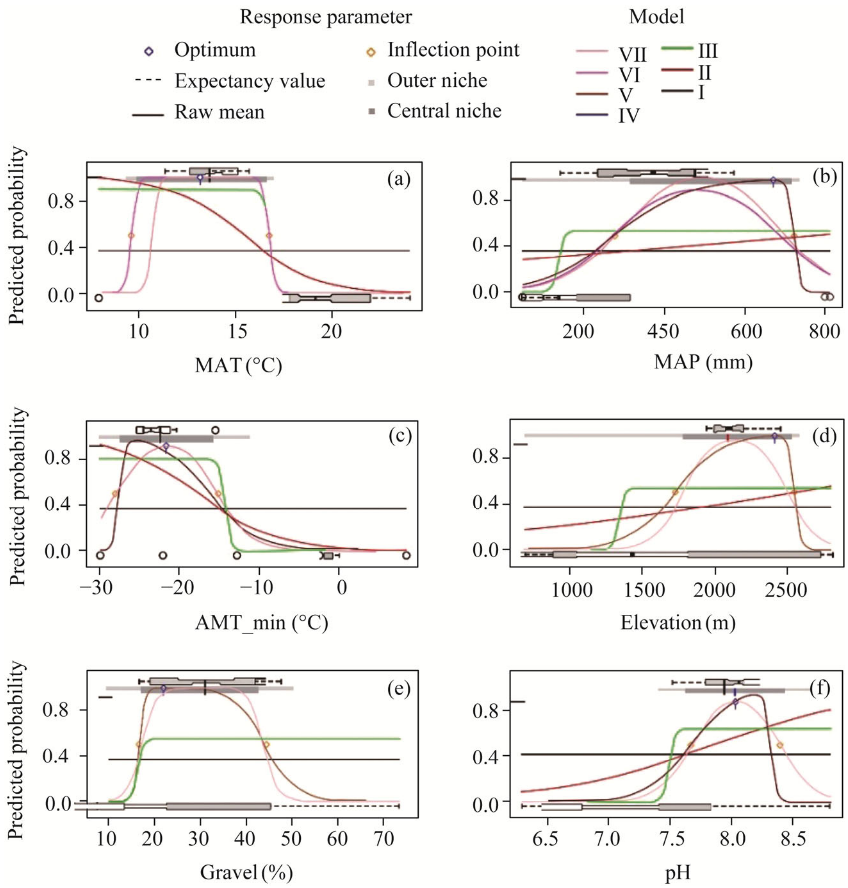

Fig. 3 Response curves and optimal presence points of *H. criniferum* with respect to environmental parameters. (a), MAT; (b), MAP; (c), AMT_min; (d), elevation; (e), gravel; (f), pH. The descriptions of Models I–VII are provided in Table 5. In the response curve plots, the upper box plots illustrate the variability of presence points, while the lower box plots represent the variability of absence points, highlighting the median and variance of the species' distribution. The gray lines reflect model uncertainty, with narrower lines indicating lower uncertainty and wider lines indicating higher uncertainty.

endangered endemic species *H. criniferum* across the arid and semi-arid rangelands of Iran. Our findings offer valuable insights into the intricate relationships between *H. criniferum* and key environmental variables, crucial for its conservation and management. Specifically, MAP, MAT, AMT_min, elevation, and soil characteristics (e.g., gravel and pH) emerged as the most influential parameters shaping the distribution of *H. criniferum* (Sheikhzadeh et al., 2016). These results underscore the significant roles of climatic conditions and soil properties in shaping the species' distribution patterns within the study area, emphasizing the necessity of considering multiple environmental variables when assessing habitat suitability (Hayati et al., 2022).

The distribution of a plant species is influenced by a combination of intrinsic factors such as ecological tolerance, evolutionary potential, and reproductive and dispersal capabilities, as well as extrinsic factors like climate, soil properties, and interactions with pollinators (Shahbazi et al., 2017). These external factors do not act in isolation but interact and vary over space and time, making it challenging to pinpoint the most critical determinants (Berini et al., 2018; Westerband et al., 2021). Our study addresses this complexity by employing a comprehensive approach that integrates field sampling and advances statistical modeling techniques. The best subset regression analysis and HP were employed to manage multicollinearity and model complexity, providing a robust framework for identifying the key drivers of species distribution. While our study cannot capture all possible interactions and variations, it provides a foundational understanding of the

factors affecting *H. criniferum* distribution and underscores the importance of considering multiple environmental variables in habitat suitability assessments.

MAP emerged as a pivotal factor influencing the presence of *H. criniferum*, highlighting the critical role of water availability in the species' growth and survival. Our findings indicated that *H. criniferum* exhibited a nuanced response to increasing precipitation, with an incremental-decremental pattern, suggesting an adaptation to semi-arid climates (Shahbazi et al., 2017). The variability in precipitation across different habitats where *H. criniferum* is found reflects its resilience and ability to thrive under diverse climatic conditions (Dianati-Tilaki et al., 2016; Hayati et al., 2022). However, it is essential to note that seeds from populations in areas with low annual precipitation (e.g., 150 mm in Moote) may not be suitable for seeding in areas with significantly higher precipitation (e.g., 550 mm in Damane). This discrepancy suggests the possible existence of distinct ecotypes within the species, adapted to specific environmental conditions. Further research is required to explore this possibility and to better understand the species' adaptive mechanisms across varying climatic conditions.

The temperature-dependent behavior of *H. criniferum* reveals a consistent decremental trend with increasing temperatures. In its natural habitat, typically mountainous areas where winter is characterized by snow cover, the species may require a period of chilling for successful germination. This observation aligns with studies on closely related species, such as *Hedysarum boreale* Nutt, where germination rates decline with increasing temperatures (Redente, 1982; Xue et al., 2012). This temperature sensitivity underscores the importance of preserving specific microclimates within the range of *H. criniferum* to ensure successful reproduction and long-term survival.

Elevation, a critical topographic factor, profoundly influences the distribution of *H. criniferum*. This species predominantly thrives in highlands and mountainous terrain, displaying a marked preference for elevation characterized by significant variations in temperature, precipitation, and habitat structure. These preferences are consistent with broader ecological principles that connect elevation gradients to variations in temperature, humidity, wind speed, and sunlight exposure, all of which are crucial in shaping plant ecophysiology (Zhang and Dong, 2010; Davis et al., 2018). Highland, often less accessible for grazing or human intervention, fosters greater plant diversity (Gao et al., 2012), thereby enhancing the likelihood of *H. criniferum* occurrence.

Soil characteristics, particularly gravel content and pH level, play a crucial role in shaping the distribution of *H. criniferum*. A gravel content exceeding 40.0% was associated with a decrease in the likelihood of species presence. This result suggests that while gravel aids soil ventilation, excessive gravel hinders plant growth by affecting water retention and root penetration. Similarly, the preference of *H. criniferum* for alkaline soils aligns with the influence of soil pH on nutrient solubility, directly affecting plant growth (Hartemink and Barrow, 2023). The interaction between soil pH and nutrient availability is crucial, as it directly affects the physiological processes of *H. criniferum*, particularly its nutrient uptake efficiency and overall health.

4.2 Methodological insights and model comparisons

Previous studies, such as Hayati et al. (2022), utilized PCA to identify factors influencing the occurrence of *H. criniferum*. However, PCA does not provide a direct and detailed assessment of the relationships between individual environmental variable and species distribution. To build upon these efforts and gain deeper insights into the habitat requirement of *H. criniferum*, we employed the best subset regression analysis and HP. The best subset regression analysis allowed us to select the most predictive variables from a larger pool, effectively identifying key drivers of species distribution while addressing challenges like multicollinearity and model complexity (James et al., 2013). HP further refined our understanding by quantifying the independent contributions of each environmental factor to species distribution, aiding in the prioritization of management action and the identification of target variables for conservation intervention (Mac Nally, 1996).

The species response curves generated by the eHOF models offered valuable insights into the

ecological preference and tolerance of *H. criniferum* to various environmental variables. While these models are powerful tools for identifying tolerance range and optimal growth point, generalizing these findings to real-world conditions would benefit from further empirical validation. Nevertheless, the ability of the eHOF models to pinpoint optimal conditions enhances their utility in ecological analyses, providing essential guidance for habitat management and restoration efforts aimed at conserving *H. criniferum* populations in the study area. Notably, when comparing our findings with those of Hayati et al. (2022), who employed the GLM method, some disparities emerged. While there was relative consistency in identifying MAT, gravel content, and AMT_min as key factors influencing *H. criniferum*, discrepancies were observed in the optimal values for MAP (650 mm vs. 400 mm) and pH level (8.0 vs. 7.7). These differences highlight the impact of methodological approaches on ecological modeling outcomes. Despite these variations, our study reinforces the importance of understanding the ecological requirement of *H. criniferum* through multiple analytical frameworks, contributing valuable insight for conservation and management strategies.

The non-linear response patterns observed in *H. criniferum* to environmental factors are significant for understanding the species' ecological niche. The prevalence of unimodal response curves within the ecological niche of this species suggests a sensitivity to optimal condition (Adel et al., 2017). This phenomenon implies that *H. criniferum* thrives within a narrow range of optimal environmental condition, and beyond which its growth or distribution may decline. This sensitivity underscores the importance of protecting habitats that maintain these optimal conditions, particularly in the face of climate change and habitat degradation. Furthermore, our findings have broader implications for the conservation of *H. criniferum* and similar species. The detailed understanding of the species' environmental requirements can inform targeted conservation strategies, such as habitat restoration, assisted migration, and the protection of critical microhabitat. Additionally, this research highlights the need for ongoing monitoring and adaptive management to address the dynamic nature of ecological system and the potential impact of climate change.

4.3 Management implications

The findings of this study provide valuable insights for conservation planning and land management strategies aimed at preserving the distribution and habitat of *H. criniferum*. Conservation efforts should prioritize protecting habitats that offer suitable condition for the species, considering the significant influence of environmental factors such as MAP, MAT, elevation, gravel content, and soil pH. Given the species' sensitivity to climate variables, particularly temperature and precipitation, proactive measures are necessary to address potential impacts of climate change on its habitat. Monitoring climate trends and implementing adaptive strategies, such as habitat restoration and assisted migration, are crucial for mitigating adverse effects (Xu and Prescott, 2024).

Using insights from this study, efforts can be directed toward establishing new populations in areas with similar environmental condition that is currently unoccupied by the species. This can enhance its resilience and long-term viability amid habitat degradation and climate change challenges.

To minimize the negative impacts of grazing on *H. criniferum* and its habitat, people should carefully plan and implement grazing management practices. Considering the importance of soil characteristics in shaping the distribution of the species, people should prioritize soil conservation measures to maintain soil health and prevent erosion. Additionally, proactive efforts are needed to identify suitable areas for the cultivation and seeding of *H. criniferum* to bolster its population and ensure its long-term survival.

4.4 Future research

While this study provides significant insights into the environmental determinants of *H. criniferum* distribution, several areas warrant further investigation. Future research should explore

the potential existence of distinct ecotypes within *H. criniferum* populations, particularly in relation to variations in precipitation and temperature. Genetic studies and phenotypic assessments across different populations could provide valuable information on the species' adaptability to diverse environmental conditions. Long-term monitoring of *H. criniferum* across different habitats is essential to assess the impact of climate change on its distribution and population dynamics. Understanding the species' response to changing environmental conditions will aid in developing adaptive management strategies for its conservation.

5 Conclusions

In summary, our investigation focused on identifying the main factors determining the distribution of *H. criniferum*, a rare plant species predominantly found in the mountains of Iran, particularly in arid and semi-arid rangelands. Through our study, we identified precipitation, temperature, elevation, soil composition (specifically gravel content), and soil pH as critical determinants of *H. criniferum*'s habitat preference. The results revealed that the species' responses to these factors exhibit complex and non-linear relationships, providing a more nuanced understanding than traditional methods. The eHOF model developed in this study proved valuable for accurately predicting potential habitats conducive to the growth of *H. criniferum*, thereby supporting more effective landscape management strategies. We recommend that future researches expand to additional factors such as geological attributes, historical land use patterns, and management practices, which could further refine predictive models and enhance conservation effort. Ultimately, our findings provide actionable insights that can guide targeted conservation initiatives to preserve the specific habitats of *H. criniferum*, thereby directly contributing to the conservation of biodiversity in mountainous areas of Iran.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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